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Determining the Area of a Gastropod's Foot[1]

by

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Abstract. A photographic procedure involving the weighing of enlarged images of the foot of the prosobranch *Ilyanassa obsoleta* has been applied to the problem of determining the area of a gastropod's foot. The results have been compared with those derived from a microcomputer-assisted video scanning procedure and with estimates of pedal area employing conventional elliptical and rectangular geometric models of foot shape. Significant differences in the quantitative predictions of regression models of pedal area as a function of snail size occurred among the six techniques used to determine pedal morphometry. The photography-weighing technique was highly reliable and compared favorably with video scanning. The geometric models over- or underestimated pedal surface area differentially as a function of both the size of a snail and the selection of a width parameter for the calculation of geometric area.

INTRODUCTION

For non-pelagic motile gastropods the ventral surface of the foot is important not only for locomotion but also for the maintenance of position against the effects of gravity, wind and waves. A comprehensive understanding of gastropod pedal morphology and locomotory mechanisms might include a description of locomotory types (MILLER, 1974a), an analysis of adaptive and functional attributes (MILLER, 1974b; GAINEY, 1976; LINSLEY, 1978; PALMER, 1980), and knowledge of behavioral aspects of locomotion (BRETZ & DIMOCK, 1983; DIMOCK, in press). In such studies it is often important to have an estimate of quantitative parameters of pedal morphology. However, the measurement of fleshy, mucus-secreting morphological features of a motile soft-bodied organism may not always be readily effected.

In this paper I present a photographic approach to quantifying morphometric parameters of the foot of the marine mud snail *Ilyanassa obsoleta* (Say, 1822). The data from this technique are compared with those derived from a microcomputer-based video image analyzer, as well as calculations of conventional geometric models of pedal surface area. The photographic procedure is shown to be highly reliable. It is readily adaptable to conditions (or species?) under which standard geometric models may yield grossly inaccurate estimates of pedal morphometry.

MATERIALS AND METHODS

All specimens of *Ilyanassa obsoleta* were collected from the Newport River marshes near Morehead City, North Carolina. The foot of each of 20 animals (shell length = 9.1–18.3 mm) was photographed as a snail crawled vertically up the side of a glass aquarium. Several exposures were made of each animal and also of lined graph paper (5 mm squares) held against the inside of the same wall of the aquarium. All of the exposures were taken at the same distance from the aquarium with a 35-mm camera with close-up lenses. The exposure in which a snail's foot appeared most nearly bilaterally symmetrical was selected for printing.

Three prints of each snail's foot and seven of the graph paper were enlarged (about 6 ×) and processed identically with an automatic print processor. After the prints were dried, each image of a snail's foot was carefully cut from the photographs and weighed to 0.1 mg. The area of the pedal surface was estimated by comparison to the mean weight of a standard "1 cm^2" as determined from the prints of the graph paper. The dimensions of a snail's foot were determined by reference to the grid system of the photographs of the graph paper, with foot width being measured both as the maximum width, exclusive of the antero-lateral horns of the propodium, and the width at one-half foot length.

Each cutout image of a snail's foot was also scanned with a microcomputer-based video image analyzer (Darwin Instrument Company, Winston-Salem, NC) which utilizes an analytical video camera with appropriate digitizer to computer interface and associated software to resolve such parameters as the length, width, or area of an image (TELEWSKI *et al.*, 1983). The area of the foot was also calculated as the area of an ellipse and of a rectangle with the two measures of width described above.

The association of logarithm foot area with logarithm shell length was assessed by Pearson's product-moment

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Table 1

The magnitude and accuracy of various estimates of the pedal area of *Ilyanassa obsoleta* in reference to shell length (SL), foot length (FL), and foot width (FW) expressed both as maximum width (A) and width at one-half FL (B).

SL (mm)	FL (mm)	FW (mm)		Estimated area (mm^2)						Difference (as % of "by weight")				
		A	B	By weight	By video	By ellipse A	By ellipse B	By rectangle A	By rectangle B	Video	Ellipse A	Ellipse B	Rectangle A	Rectangle B
9.1	7.3	3.6	3.1	20.1	20.0	20.6	17.8	26.3	22.6	−0.5	+2.5	−11.4	+30.8	+12.4
10.2	7.9	4.0	3.3	23.7	23.0	24.8	20.5	31.6	26.1	−3.0	+4.6	−13.5	+33.3	+10.1
10.2	8.4	4.1	3.6	26.5	25.9	27.0	23.8	34.4	30.2	−2.3	+1.9	−10.2	+29.8	+14.0
10.9	9.6	5.3	4.8	40.6	40.8	40.0	36.2	50.9	46.1	+0.5	−1.5	−10.8	+25.4	+13.5
11.0	8.4	4.4	3.8	27.3	26.8	29.0	25.1	37.0	31.9	−1.8	+6.2	−8.1	+35.5	+16.8
12.7	10.3	5.0	4.3	40.8	40.1	40.5	34.8	51.5	44.3	−1.7	−0.7	−14.7	+26.2	+8.6
13.5	11.5	6.1	6.0	58.1	59.4	55.1	54.2	70.2	69.0	+2.2	−5.2	−6.7	+20.8	+18.8
14.2	12.1	6.2	5.6	57.9	57.8	58.9	53.2	75.0	67.8	−0.2	+1.7	−8.1	+29.5	+17.1
14.3	12.9	5.7	5.2	60.0	60.2	57.8	52.7	73.5	67.1	+0.3	−3.7	−12.2	+22.5	+11.8
14.5	12.5	5.5	5.0	54.9	54.4	54.0	49.1	68.8	62.5	−0.9	−1.6	−10.6	+25.3	+13.8
15.1	12.8	6.2	5.6	61.7	62.3	62.3	56.3	79.4	71.7	+1.0	+1.0	−8.8	+28.7	+16.2
15.2	13.7	6.3	5.8	71.5	72.8	67.8	62.4	86.3	79.5	+1.8	−5.2	−12.7	+20.7	+11.2
16.3	12.9	6.5	6.1	67.3	68.8	65.9	61.8	83.9	78.7	+2.2	−2.1	−8.2	+24.7	+16.9
16.4	12.9	6.9	6.8	73.4	74.1	69.9	68.9	89.0	87.7	+1.0	−4.8	−6.1	+21.3	+19.5
16.7	13.1	7.4	7.3	80.1	81.9	76.1	75.1	96.9	95.6	+2.2	−5.0	−6.2	+21.0	+19.4
16.8	15.5	6.7	6.2	84.7	83.3	81.6	75.5	103.9	96.1	−1.7	−3.7	−10.9	+22.7	+13.5
17.3	16.0	7.6	6.9	95.2	95.3	95.5	86.7	121.6	110.4	+0.1	+0.3	−8.9	+27.7	+16.0
17.3	14.0	7.1	6.7	81.5	80.4	78.1	73.7	99.4	93.8	−1.3	−4.2	−9.6	+22.0	+15.1
17.6	16.1	7.0	6.4	88.4	88.2	88.5	80.9	112.7	103.0	−0.2	+0.1	−8.5	+27.5	+16.5
18.3	15.3	7.9	7.4	96.5	96.4	94.9	88.9	120.9	113.2	−0.1	−1.7	−7.9	+25.3	+17.3
										$\bar{X}$ = −0.1	−1.1	−9.7	+26.0	+14.9

correlation for each of the six measures of foot area. The slopes and elevations of the resulting regression equations were compared by analysis of covariance (ANOCOVA); significant differences among the regressions were resolved with Student-Newman-Keuls multiple range test (SNK; ZAR, 1974).

RESULTS

All weights of a standard cm^2 of the enlarged photographic prints were within 1.8% of the mean (n = 7); no print of a snail's foot varied more than 2.0% from the mean weight (n = 3) for that animal.

The morphometric data for 20 specimens of *Ilyanassa obsoleta* are presented in Table 1. The video scan procedure and the weighing technique were virtually identically precise for determining the area of the image of a snail's foot. However, the elliptical and rectangular models consistently over- or underestimated the area of pedal surface relative to the weighing technique (Table 1). When the area of the foot was modeled as an ellipse, both the sign and the magnitude of the error in estimating pedal area were influenced by the way the width of the foot had been determined.

There was no consistent pattern of the error of estimating pedal area with the elliptical model when the area was calculated using the maximum width. However, when the width was taken as that at one-half of foot length, the error varied with the size of the snail; the coincidence of the elliptical model of pedal area with the area determined by the weighing technique was positively correlated with shell length ($r = 0.449$, df = 18, P = 0.047). Thus, the area of the foot of a small specimen of *Ilyanassa obsoleta* was less accurately modeled by an ellipse when foot width was measured at one-half foot length (Table 1), but the precision of the elliptical model increased with increasing snail size.

The rectangular geometric model overestimated pedal area by as much as 35% (Table 1). In contrast to the elliptical model, the greatest deviation between the area calculated with the rectangular model and that determined by weighing occurred when the width of the foot was taken as the maximum width (Table 1). The magnitude of that overestimation was negatively correlated with snail size ($r = -0.590$, df = 18, P = 0.006). However, when the width at one-half foot length was used to calculate rectangular area, the error of overestimation was positively correlated with shell length ($r = 0.478$, df = 18, P = 0.033; Table 1). Thus, both the magnitude and the size-specific characteristics of the error in estimating pedal area were functions of the parameters used in the geometric models.

Although both the length and the width (and consequently the area) of the foot of *Ilyanassa obsoleta* increased

Table 2

The area (FA) of the foot of *Ilyanassa obsoleta* as a function of shell length (SL): a comparison of techniques.

Procedure for determining area	Regression equation	r^2	df	P
Weighing	*log FA = 2.23 log SL − 0.83	0.956	18	<0.001
Video	*log FA = 2.27 log SL − 0.86	0.953	18	<0.001
Ellipse (A) (maximum foot width)	*log FA = 2.14 log SL − 0.72	0.963	18	<0.001
Ellipse (B) (foot width at ½ foot length)	log FA = 2.29 log SL − 0.94	0.957	18	<0.001
Rectangle (A) (maximum foot width)	log FA = 2.14 log SL − 0.61	0.963	18	<0.001
Rectangle (B) (foot width at ½ foot length)	*log FA = 2.29 log SL − 0.83	0.957	18	<0.001

ANOCOVA:

H_o: Slopes of regression equations are equal	F = 0.39	df = 5,108	P = 0.428
H_o: Elevations of regressions are equal	F = 28.1	df = 5,108	P < 0.001

* Indicates regressions that are not significantly different (SNK; P > 0.05)

with increasing shell length (Table 1), the apparent quantitative association of pedal area with shell length varied with the technique employed in estimating that area (Table 2).

DISCUSSION

Although a quantitative assessment of foot morphometry may be central to an understanding of some aspects of the biology of gastropods, the techniques for determining such parameters as area of the pedal surface may either simply not be identified (GAINEY, 1976) or may be only incompletely described (MILLER, 1974b). For example, in one of the more thorough analyses of the adaptive design of prosobranch pedal morphology, MILLER (1974b) simply states that the length and width of a snail's foot "were measured" and that area of the foot was calculated as the area of a rectangle or of an ellipse "depending upon the shape of the foot." No information is provided as to how the linear dimensions of a snail's foot actually were physically determined nor upon what basis a decision was made about which model of the shape of a gastropod's foot was most appropriate for determining the pedal area of a given snail (MILLER, 1974b). These parameters were then used by Miller to characterize the pedal morphometry of an array of species and to relate these morphometric attributes to functional and adaptive parameters of foot form.

It is clear from the present study that not all techniques for the determination of pedal morphometry yield equally reliable estimates of the quantitative properties of gastropod feet. Aside from difficulty in the mechanics of measuring linear features of a motile, fleshy structure, there may also be significant consequences of the selection of a geometric model for estimating an important parameter such as area of the foot. If one assumes that the photography-weighing procedure yielded a good measure of foot morphometry, then the alternative geometric models for determining pedal surface area can be compared. One obvious conclusion is that a rectangular model of pedal surface is not a very accurate depiction of the morphology of the foot of *Ilyanassa obsoleta*. For all sizes of snails examined, the rectangular model overestimated pedal area (Table 1). The closest correspondence between the rectangular model and the shape of the foot of *I. obsoleta* occurred among the smaller snails when the rectangular dimensions were based upon width of the foot as measured at one-half foot length. However, even under those conditions the rectangular model overestimated pedal surface area by more than 10% (Table 1).

Overall, an elliptical model provided a reasonably good estimate of pedal surface area for *Ilyanassa obsoleta*, but only when the width of the foot was taken as the maximum width (Table 1). When the width was considered as that at one-half foot length [which was Miller's approach (MILLER, 1974b)], the elliptical model underestimated pedal area. The extent of underestimation was greatest among the smaller snails (Table 1), an observation that is consistent with the better relative fit of the rectangular model to the same animals. Thus, although the ratio of foot length to maximum foot width is constant over a range of shell lengths for *I. obsoleta* (DIMOCK, in press), the shape of this snail's foot does change with the size of the animal. Therefore, one would be in error to assume that a single geometric model adequately describes the morphology of this mud snail's foot irrespective of shell size. It is likely that similar size-specific morphometric relationships exist among other species of gastropods.

An analysis of the various regressions of the area of the foot of *Ilyanassa obsoleta* on shell length confirms the supposition that certain techniques are more satisfactory than others for quantifying pedal morphology (Table 2). Although each procedure for estimating area employed in this study would reveal that the area of this snail's foot is a positive function of shell length, the precise quantitative characteristics of that association depend upon how specific morphological parameters are determined. Such quantitative relationships are influenced not only by the selection of a particular geometric model of foot morphology, but also by the way in which a linear dimension may be defined. The use of a procedure such as the photography-weighing technique has the added advantage of obviating any subjective evaluation of whether or not one geometric model is more appropriate than another (MILLER, 1974b).

The weighing of photographic images of snail feet and the microcomputer assisted video camera scanning of the same images yielded quite comparable measures of the original surface area of the foot of *Ilyanassa obsoleta*. Clearly, the photography-weighing procedure is adaptable to numerous laboratory contexts and requires much less sophisticated equipment than does the video scanning system. This photo-morphometric procedure should be useful in an assortment of investigations of various aspects of the biology of gastropods.

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